Z. Säugetierkunde 55 (1990) 239–243 © 1990 Verlag Paul Parey, Hamburg und Berlin ISSN 0044-3468

# Cold-adaptive modifications and torpor in the Cretan Spiny mouse (*Acomys minous* Bate, 1905)

By INKEN BARFOD and W. WÜNNENBERG

Department of Zoophysiology, Christian-Albrechts-University of Kiel, FRG

Receipt of Ms. 23. 2. 1989 Acceptance of Ms. 23. 5. 1989

## Abstract

Studied the effects of cold exposure, photoperiod, and food availability on metabolic rate and body temperature in the Cretan spiny mouse (*Acomys minous*). In animals with food ad lib. exposure to ambient temperatures (Ta) auf 10 °C led to a gradual increase of the nychthemeral fluctuations of metabolic rate and body temperature. Within 3 days metabolic rates and body temperatures measured during the activity phase (night) were shifted to higher values while the corresponding values measured during the day remained unchanged. These effects which are regarded as cold adaptive modifications do not depend on the photoperiod. Food restriction (at Ta = 20 °C) induced torpor with a decline of the colon temperatures to 25.9  $\pm$  1.6 °C (mean  $\pm$  SD) and a decrease of the metabolic rates to 50 % of the initial values.

Experiments suggest that *Acomys minous* can cope with unfavourable low Ta by an increase of metabolism during the activity phase or by entry into torpor depending on food availability.

# Introduction

In endothermic animals prolonged or repeated exposure to cold may cause adaptive modifications which reduce the physiological strain produced by the stressful environmental component (cf. SIMON 1987; BRÜCK 1986). These modifications may consist of an enhancement of the thermal insulation, e.g. growth of fur, or of various alterations in the thermoregulatory system. Latter effects of chronic could exposure, generally denoted as functional modifications, may be traced back to mainly two basic mechanisms: 1. changes in the capacity of the thermogenetic effector systems by development or enhancement of non-shivering thermogenesis (NST), and 2. changes in the regulatory characteristics, e.g. deviations of the threshold temperatures for the elicition of regulatory heat production (cf. BRÜCK 1986).

Beside the development of specific adaptive modifications further strategies are known which enable some animals to cope with unfavourable environmental conditions. In many small mammalian species with body weights less than 100 g exposure to low ambient temperatures (Ta) is accompanied with the occurrence of shallow torpor which is characterized by a controlled lowering of the set point for body temperature regulation with a corresponding reduction in metabolic rate. In most species, however, induction of torpor is not directly caused by the low Ta. In the Djungarian hamster (*Phodopus sungorus*) daily torpor is a seasonal phenomenon, i.e. changes of the photoperiod is the most important factor in the control of torpor (HELDMATER and STEINLECHNER 1981). In pocket mice (*Perognathus californicus, P. longimembris, P. hispidus*) and in the kangaroo mouse (*Microdipodops pallidus*) there is a clear correlation between the incidence of torpidity and the availability of food (TUCKER 1962; BARTHOLOMEW and CADE 1957; WANG and HUDSON 1970; BARTHOLOMEW and MAC MILLEN 1961). In bats, on the other hand, torpor seems to be caused by the nychthemeral fluctuations of Ta (KULZER 1965).

Under chronic cold exposure occurrence of daily torpor which usually lasts 8-12 h does

U.S. Copyright Clearance Center Code Statement: 0044-3468/90/5504-0239 \$ 02.50/0

not exclude the possibility to develop cold adaptive modifications. It was the aim of the present experiments to study the environmental factors that cause cold adaptation and torpor in the Cretan spiny mouse.

## Materials and methods

Experiments were carried out in adult male and female Cretan spiny mice (*Acomys minous* Bate, 1905) wheighing 25–39 g. They were bred and raised in our laboratory. Animals were fed sunflower seeds, peanuts, oats, corn, Purina rat chow, and water ad libitum.

Animals were randomly divided into three groups which were kept under different environmental conditions for at least 8 weeks. One group was kept at  $Ta = 20 \pm 1$  °C and a 16:8 light-dark cycle. The other groups were exposed to  $10 \pm 1$  °C and to either a long (LD 16:8) or a short (LD 8:16) photoperiod. Cold exposed animals were housed in individual cages.

As a measure of metabolic rate CO<sub>2</sub>-production was determined by the open system method by means of a climatized metabolic chamber as described previously (BRÜCK and WÜNNENBERG 1965). Within this metabolic chamber the unrestrained animal was supplied with food, water, and some nesting material with the exception of the tests in which the effects of starvation were studied.

Deep colon temperature (Tcol) was measured with fine thermocouples.

The U-test of WILCOXON, MANN, and WHITNEY was used for statistical analysis.

## Results

In all groups of Cretan spiny mice minimum observed metabolic rates (MOMR) and body temperatures showed a nychthemeral rhythm with maximum values during the night. In animals kept at Ta = 20 °C average CO<sub>2</sub>-production during the day was  $32.7 \pm 7.0 \,\mathrm{ml} \cdot \mathrm{kg}^{-1} \cdot \mathrm{min}^{-1}$  and  $43.1 \pm 8.2 \,\mathrm{ml} \cdot \mathrm{kg}^{-1} \cdot \mathrm{min}^{-1}$  during the night. As soon as animals of this group (N = 8) were exposed to Ta = 10 °C, CO<sub>2</sub>-production increased to  $53.4 \pm 5.4 \,\mathrm{ml} \cdot \mathrm{kg}^{-1} \cdot \mathrm{min}^{-1}$  and  $70.6 \pm 6.0 \,\mathrm{ml} \cdot \mathrm{kg}^{-1} \cdot \mathrm{min}^{-1}$ , respectively (Tab. 1). As

Table 1. Effects of cold exposure and photoperiod on minimum observed metabolic rate in Acomys minous

Cold exposure (Ta = 10 °C)	Photoperiod	CO <sub>2</sub> -production ( day	$ml \cdot kg^{-1} min^{-1})$ night	n
1 <sup>st</sup> day 2 <sup>nd</sup> day 3 <sup>rd</sup> day 8 weeks 8 weeks	LD 8:16 LD 8:16 LD 8:16 LD 8:16 LD 8:16 LD 16: 8	$53,4 \pm 5,4 \\ 53,5 \pm 7,2 \\ 54,2 \pm 6,9 \\ 54,0 \pm 8,7 \\ 61,1 \pm 10,7 \\ \end{cases}$	$\begin{array}{rrrr} 70,6 \ \pm \ 6,0 \\ 75,8 \ \pm \ 6,8 \\ 77,2 \ \pm \ 7,8 \\ 74,1 \ \pm \ 7,5 \\ 85,3 \ \pm \ 15,6 \end{array}$	8 8 7 8 5

(mean  $\pm$  SD, n = number of animals)

demonstrated in Fig. 1 a continuation of the cold exposure has a considerable effect on the nychthemeral fluctuations of MOMR. While at the 3<sup>rd</sup> day of cold exposure average CO<sub>2</sub>-production during the day did not show a significant change in comparison to the 1<sup>st</sup> day, the corresponding value measured during the night increased to 77.2  $\pm$  7.8 ml · kg<sup>-1</sup> · min<sup>-1</sup>. Similar effects of chronic cold exposure were observed when Tcol was measured (Fig. 1, lower part). Colon temperatures determined during the night continuously increased from 35.4  $\pm$  0.9 °C (2<sup>nd</sup> day of exposure) to 36.9  $\pm$  0.3 °C (4<sup>th</sup> day of exposure). Temperature values measured during the day, however, did not change significantly in the course of chronic cold exposure.

These changes of metabolic rate which developed within three days of cold exposure were not enhanced when the animals were adapted to  $Ta = 10 \degree C$  for 8 weeks (Tab. 1).



Cold-adaptive modifications and torpor in the Cretan Spiny mouse

*Fig. 1.* Course of CO<sub>2</sub>-production and colon temperature (mean  $\pm$  SD) in *Acomys minous* exposed to Ta = 10 °C and a 8:16 light/dark cycle for several days. Shaded areas indicate scotophase

Furthermore, studies in 5 animals that were kept at Ta = 10 °C and a long photoperiod indicate that the increment of the nychthemeral metabolic fluctuations is mainly caused by the cold exposure (Tab. 1).

The effects of chronic cold exposure on MOMR and Tcol described above were all determined in animals that had free access to food and water. Food restriction (40 h) led to quite different results. Under this condition all animals (N = 23) entered into torpor during the day-time. Though cold stress was moderate (Ta = 20 °C) Tcol declined to  $25.9 \pm 1.6$  °C and MOMR decreased but about 50% of the initial value (Fig. 2). All animals quickly recovered after termination of the starvation experiments.

# Discussion

It is well known that cold adaptation leads to an increase of the metabolic rate. At thermoneutral Ta as well as under cold stress cold-adapted dogs, rabbits, and rats, e.g., had considerable higher metabolic rates than the corresponding control animals (cf.



Fig. 2. Starvation induced torpor in *Acomys minous* at TA = 20 °C. Shaded areas indicate scotophase. (mean  $\pm$  SD)

PRECHT et al. 1973). Our studies indicate that in *Acomys minous* total energy metabolism, related to 24 hours, only slightly increases during cold adaptation as a significant increase of the  $CO_2$ -production only occurs during the night hours. This cold-adaptive modification of the metabolic rate which seems to be independent of the photoperiod favours the adjustment of high body temperatures during the night when the Cretan spiny mice are active.

Development of adaptation, however, is not the only mode of coping with unfavourable environmental conditions. Our studies further show that *Acomys minous* exposed to a moderate cold stress enter into torpidity when food availability is restricted. Comparable results were obtained by studies in *Acomys cahirinus* (Müller et al. 1987) as well as by numerous investigations in other species of rodents (cf. LYMAN et al. 1982; HUDSON 1978). Thus, our studies also support the hypothesis that torpor is used in "energy emergency" situations when energy availability is restricted relative to expenditures (HAINSWORTH and Wolf 1978; Tucker 1966).

### Zusammenfassung

#### Kälteadaptative Modifikationen und Torpor bei der Kreta-Stachelmaus (Acomys minous Bate)

Es wurden die Effekte niedriger Umgebungstemperaturen (Ta), der Photoperiode und des Nahrungsangebotes auf den Stoffwechsel und die Körperkerntemperaturen der Stachelmaus (Acomys minous) untersucht. Bei Tieren, denen Futter ad lib. zur Verfügung stand, führte Kälteexposition (Ta = 10 °C) bereits nach drei Tagen zu einer Zunahme der diurnalen Fluktuationen des Stoffwechsels und der Körpertemperaturen. Dabei stiegen die während der Aktivitätsphasen (Nacht) gemessenen Stoffwechsel- und Temperaturwerte an, während sich die entsprechenden Werte der Ruhephasen (Tag) nicht signifikant änderten. Diese Effekte, die als kälteadaptative Modifikationen angesehen werden, traten sowohl unter Kurztag- als auch unter Langtagbedingungen auf. Durch Nahrungsmangel (bei TA = 20 °C) wurde dagegen Torpor induziert. Die Körperkerntemperaturen der Tiere sanken auf 25.9  $\pm$  1.6 °C (Mittelwert  $\pm$  SD) ab, die Stoffwechselraten erreichten nur noch 50 % der Ausgangswerte.

Die vorliegenden Untersuchungen zeigen, daß bei Acomys minous eine mehrtägige Kältebelastung - in Abhängigkeit vom Nahrungsangebot – entweder zu einer Steigerung des Stoffwechsels (Kälteadaptation) oder zu einer deutlichen Stoffwechselreduktion (Torpor) führt.

### References

- BARTHOLOMEW, G. A.; CADE, T. Y. (1957): Temperature regulation, hibernation, and aestivation in the little pocket mouse. Perognathus longimembris. J. Mammalogy 38, 60-72.
- BARTHOLOMEW, G. A.; MACMILLEN, R. E. (1961): Oxygen consumption, estivation, and hibernation in the kangaroo mouse, Microdipodops pallidus. Physiol. Zool. 34, 177-183.
- Вкüск, К. (1986): Basic mechanisms in thermal long-term and short-therm adaptation. In: Thermal relations in animals and man. Ed. by H. LAUDIEN. Stuttgart, New York: G. Fischer, BIONA report 4, 93-100.
- BRÜCK, K.; WÜNNENBERG, B. (1965): Über die Modi der Thermogenese beim neugeborenen Warmblüter. Untersuchungen am Meerschweinchen. Pflügers Arch. ges. Physiol. 282, 362-375.
- HAINSWORTH, F. R.; WOLF, L. L. (1978): The economics of temperature regulation and torpor in nonmammalian organisms. In: Strategies in cold: Natural torpidity and thermogenesis. Ed. by L. C. H. WANG and J. W. HUDSON. New York: Academic Press, 147–184.
- HELDMAIER, G.; STEINLECHNER, S. (1981): Seasonal pattern and energetics of short daily torpor in the Djungarian hamster, Phodopus sungorus. Oecologia 48, 265-270.
- HUDSON, J. W. (1978). Shallow, daily torpor: a thermoregulatory adaptation. In: Strategies in cold: Natural torpidity and thermogenesis. Ed. by L. C. D. WANG and J. W. HUDSON. New York: Academic Press, 67–108. KULZER, E. (1965): Temperaturregulation bei Fledermäusen (*Chiroptera*) aus verschiedenen Klimazo-
- nen. Z. vgl. Physiol. 50, 1-34.
- LYMAN, C. P.; WILLIS, J. S.; MALAN, A.; WANG, L. C. H. (1982): Hibernation and torpor in mammals and birds. New York: Academic Press.
- Müller, E. F.; Pfender, P.; Beck, M. (1987): Hunger-induzierter Torpor bei Wüstenrennmäusen (Gerbillus perpadillus) und Stachelmäusen (Acomys cahirinus). Z. Säugetierkunde (Suppl.) 52, 29.
- PRECHT, H.; CHRISTOPHERSEN, J.; HENSEL, H.; LARCHER, W. (1973): Temperature and life. Berlin, Heidelberg, New York: Springer. SIMON, E. (1987): Glossary of terms for thermal physiology. Pflügers Arch. 410, 567-587.
- TUCKER, V. A. (1962): Diurnal torpidity in the California pocket mouse. Science 136, 380-381.
- TUCKER, V. A. (1966): Diurnal torpor and its relation to food consumption and weight changes in the California pocket mouse Perognathus californicus. Ecology 47, 245-252.
- WANG, L. C. H.; HUDSON, J. W. (1970): Some physiological aspects of temperature regulation in the normothermic and torpid hispid pocket mouse, Perognathus hispidus. Comp. Biochem. Physiol. 32, 275-293.
- Authors' address: INKEN BARFOD, Prof. Dr. WOLF WÜNNENBERG, Zoologisches Institut, Christian-Albrechts-Universität, Olshausenstraße 40, D-2300 Kiel, FRG